

ESTIMATING STATE-TRANSITION PROBABILITIES FOR UNOBSERVABLE STATES USING CAPTURE–RECAPTURE/RESIGHTING DATA

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Abstract. Temporary emigration was identified some time ago as causing potential problems in capture–recapture studies, and in the last five years approaches have been developed for dealing with special cases of this general problem. Temporary emigration can be viewed more generally as involving transitions to and from an unobservable state, and frequently the state itself is one of biological interest (e.g., “nonbreeder”). Development of models that permit estimation of relevant parameters in the presence of an unobservable state requires either extra information (e.g., as supplied by Pollock’s robust design) or the following classes of model constraints: reducing the order of Markovian transition probabilities, imposing a degree of determinism on transition probabilities, removing state specificity of survival probabilities, and imposing temporal constancy of parameters. The objective of the work described in this paper is to investigate estimability of model parameters under a variety of models that include an unobservable state. Beginning with a very general model and no extra information, we used numerical methods to systematically investigate the use of ancillary information and constraints to yield models that are useful for estimation. The result is a catalog of models for which estimation is possible. An example analysis of sea turtle capture–recapture data under two different models showed similar point estimates but increased precision for the model that incorporated ancillary data (the robust design) when compared to the model with deterministic transitions only. This comparison and the results of our numerical investigation of model structures lead to design suggestions for capture–recapture studies in the presence of an unobservable state.

Key words: capture–recapture models; deterministic transitions; model constraints; multi-state models; nonbreeders; robust design; temporary emigration; unobservable state.

INTRODUCTION

It is not unusual in ecology to think of animals being characterized by state variables that influence fitness components (e.g., survival probabilities) and that are dynamic over time (e.g., McNamara and Houston 1996). Potentially relevant state variables include size, physiological condition, reproductive status (e.g., breeder or nonbreeder), behavioral state, and location. The association between such state variables and demographic vital rates is important to life history theory (e.g., McNamara and Houston 1996) as well as to stage-based population modeling (e.g., Sauer and Slade 1987, Caswell 2001). If animals and their associated state variables can be observed at will (with probability 1) over time, then it is a straightforward matter to estimate state-specific survival and transition probabilities.

For sampling at discrete periods where animals cannot be observed at will, Arnason (1972, 1973) provided a basic approach for estimating state-specific survival, transition, and detection probabilities from open-model capture–mark–recapture (CMR) data. This basic approach has been used for estimation with state variables such as body mass (Nichols et al. 1992) and breeding status (Nichols et al. 1994, Cam et al. 1998), as well

as for studies of animal movement among multiple locations (Hestbeck et al. 1991, Schwarz et al. 1993, Brownie et al. 1993, Spendeelow et al. 1995). The approach of Arnason (1972, 1973), and most of the cited applications, treats state transitions as a first-order Markov process, where the probability that an animal is alive and in state s at time $t + 1$ depends on the state of the animal at time t . Brownie et al. (1993) presented a “memory model” that allows the transition probability between t and $t + 1$ to depend on state of the animal at times t and $t - 1$.

An assumption underlying these standard, multi-state modeling approaches is that whatever state an animal is in at a given sampling period, there is a non-negligible probability that it will be observed; i.e., the animal might not be observed, but it can be. When the animal is not observed, these multi-state models account for the probabilities that it is in each of the possible states. Under these models, transition to a state outside of the set of observable states is assumed to be permanent and is confounded with mortality.

Transition to an unobservable state and then back to an observable state is a possibility in some sampling situations and is generally referred to as temporary emigration in the CMR literature (e.g., Seber 1982, Kendall et al. 1997, Kendall 1999). Methods for estimating movement to and from an unobservable state include several ecological interpretations of an unob-

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servable state. Kendall et al. (1997) considered small-mammal studies in which, in one case, the distribution of traps did not envelope the range of all animals in the population, so an animal temporarily located outside the sampled area was in an unobservable state. In the other small-mammal example of Kendall et al. (1997), some animals were in torpor (the unobservable state) and thus unavailable for capture. Kendall and Nichols (1995), Schwarz and Stobo (1997), and Kendall and Bjorkland (2001) treated the cases of Snow Geese (*Anser caerulescens*), grey seals (*Halichoerus grypus*), and hawksbill sea turtles (*Eretmochelys imbricata*), respectively, where breeders can be captured and observed, but where all animals of breeding age do not breed every year (unobservable state is “non-breeder”). One can also envision the case of a metapopulation in which entire patches, breeding colonies, etc. are inaccessible to sampling or are unknown; thus, animals in these locations are unobservable. These sampling situations are very general in the sense that transition probabilities to and from the unobservable state are fully stochastic. In each case, Pollock’s (1982) robust design provides the necessary information to estimate transitions, assumed to be from a first-order Markov process.

Methods using open-population modeling without the robust design have also been developed recently for estimating temporary emigration in situations in which transitions to or from the unobservable state are partially deterministic. The age-specific breeding models of Clobert et al. (1994; also see Williams et al. 2002, Spindel et al. 2002; J.-D. Lebreton, J. E. Hines, R. Pradel, J. D. Nichols, and J. A. Spindel, *unpublished manuscript*) consider the problem of sampling breeders only (young nonbreeders are unobservable). These models permit estimation of age-specific probabilities of transition from nonbreeder to breeder only because they specify an age at which that probability is assumed to be 1.0 (all animals are assumed to begin breeding by a certain age) as well as an age before which that probability is assumed to be 0 (breeding is not possible before a certain age), and because they assume that the breeder to nonbreeder transition probability is 0. Because of these deterministic transitions, it is possible to estimate probabilities of transition from nonbreeder to breeder for specified ages in the absence of the robust design. Related approaches of Pradel et al. (1997) and Schwarz and Arnason (2000) also permit estimation of age-specific breeding probabilities in the case in which breeder to nonbreeder transitions are not possible. Fujiwara and Caswell (2002) consider a situation similar to that investigated by Clobert et al. (1994) and Williams et al. (2002), but relax the assumption that all animals must breed by a certain age. Fujiwara and Caswell (2002) also consider the situation in which nonbreeders are unobservable, and in which a breeder in one year cannot breed in the next year (Kendall and Bjorkland 2001 use the robust

design for this case), or possibly in the next two years. Fujiwara and Caswell (2002) discovered that, in some cases, transitions to and from these unobservable states can be estimated without the robust design when parameters are set constant across time and when survival parameters of some states are set equal.

In this paper, we consider the general problem of estimation for single-age models with an unobservable state. We begin with a model with an unobservable state that is more general than any of those just considered, but whose special cases intersect with these published methods. Estimation is not possible under this general model with standard, open-model CMR data. We then look for special cases of this intractable model that are both biologically realistic and whose parameters are estimable. Specifically, we consider four approaches used by previous workers (Clobert et al. 1994, Kendall et al. 1997, Fujiwara and Caswell 2002) to obtain estimates under such models. One approach, the robust design, relies on ancillary data to estimate detection probabilities for observable states. The other three approaches all involve imposition of constraints on the general model structure: deterministic transitions, equal survival probabilities for some states, and temporal constancy of parameters. For each special case considered, we are interested in whether the parameters are fully estimable (with the possible exception of the usual confounding of parameters for the last time period). We present biological examples for key models that can provide estimators, focusing on cases in which breeders are observable and nonbreeders are not.

MODEL ASSESSMENT

General model

We begin with a multinomial model that is too general (i.e., has too many parameters) to be directly useful for estimation. The model contains two states, one observable (denoted as O) and one unobservable (U). We consider movement to be a special case of a second-order Markov process. The probability that an animal that survives to time $t + 1$ is in the observable state at that time depends on whether or not it was in the observable state at time t (ψ_t^{OO}). If it was not observable at t , then the probability it is observable at $t + 1$ depends on whether it was observable at $t - 1$ (ψ_t^{UO}) or not (ψ_t^{UU}).

We model survival as state dependent, where the probability of survival from time t to $t + 1$ depends on whether the animal was in the observable state at time t (S_t^O) or not (S_t^U). The probability that an animal is detected at time t , given that it is observable, is simply modeled as a function of time (p_t^*). Using model notation similar to that of Lebreton et al. (1992), we designate this model as ($\psi_t^{OO}, \psi_t^{UO}, \psi_t^{UU}, S_t^O, S_t^U, p_t^*$). We illustrate the structure of this model with examples of expected cell frequencies for a four-period study, based

on releasing R_t animals in the observable state at each time and one detection period per time period of interest:

$$E(m_{12}|R_1) = R_1 S_1^O \psi_1^{OO} p_2^*$$

$$E(m_{13}|R_1) = R_1 S_1^O [\psi_1^{OO}(1 - p_2^*) S_2^O \psi_2^{OO}$$

$$+ (1 - \psi_1^{OO}) S_2^U \psi_2^{UO}] p_3^*$$

$$E(m_{14}|R_1) = R_1 S_1^O [\psi_1^{OO}(1 - p_2^*) S_2^O \psi_2^{OO}(1 - p_3^*) S_3^O \psi_3^{OO}$$

$$+ \psi_1^{OO}(1 - p_2^*) S_2^U (1 - \psi_2^{OO}) S_3^U \psi_3^{UO}$$

$$+ (1 - \psi_1^{OO}) S_2^U \psi_2^{UO}(1 - p_3^*) S_3^O \psi_3^{OO}$$

$$+ (1 - \psi_1^{OO}) S_2^U (1 - \psi_2^{OO}) S_3^U \psi_3^{UO}] p_4^*$$

$$E(m_{23}|R_1) = R_2 S_2^O \psi_2^{OO} p_3^*$$

$$E(m_{24}|R_2) = R_2 S_2^O [\psi_2^{OO}(1 - p_3^*) S_3^O \psi_3^{OO}$$

$$+ (1 - \psi_2^{OO}) S_3^U \psi_3^{UO}] p_4^*$$

$$E(m_{34}|R_3) = R_3 S_3^O \psi_3^{OO} p_4^*$$

where m_{th} is the number of the R_t animals released at time t that are next detected at time h . Note that the superscript O is omitted from the R_t and m_{th} statistics because animals must be in this state to be detected. Using the expression for $E(m_{14}|R_1)$ as an example, each term within brackets represents a different pattern of observability (i.e., availability for detection) between being released at time 1 and next detected at time 4. The patterns for each of the four terms are: observable at times 2 and 3, observable at time 2 but not time 3, unobservable at time 2 but observable at time 3, and unobservable at times 2 and 3, respectively.

Special cases

We consider special cases of this model that can be derived by imposing constraints that partially or completely ignore the Markovian structure. To make movement first-order Markovian, we set $\psi_t^{UO} = \psi_t^{UO'}$. To remove the state-dependent structure completely, we set $\psi_t^{OO} = \psi_t^{UO} = \psi_t^{UO'}$ for movement or $S_t^O = S_t^U$ for survival. We also consider models in which any of these parameters could be constant across time, denoted by using “.” to replace the subscript “ t ”. Finally, based on work by Kendall and Bjorkland (2001) and Fujiwara and Caswell (2002), we included cases in which transitions are partially deterministic, e.g., where breeders in year t become obligate nonbreeders in year $t + 1$ (i.e., $\psi_t^{OU} = 1$) or in both years $t + 1$ and $t + 2$.

For detection probability p_t^* , we consider scenarios where these nuisance parameters are estimated from the standard data available for CMR models of open populations; i.e., one observation period per time period of interest. We also consider the case where these detection probabilities are estimated using extra information. In this regard, we focus on the extra information provided by Pollock’s robust design (Pollock 1982, Pollock et al. 1990), where there are multiple

observation periods per time period of interest. In this case, we assume that state transitions occur between the last observation period in time period t and the first observation period in $t + 1$ (immediately before time period $t + 1$ if $S_t^O \neq S_t^U$).

Methods

For each model, we used the analytic-numeric method described by Burnham et al. (1987; see also Carrothers 1973, Nichols et al. 1981) to approximate the expected value of each estimator, and thus to determine if the parameters are estimable. Expected cell frequencies for the m_{th} statistics under the appropriate multinomial model were computed based on known parameter values and specified R_t . Those frequencies were then treated as data and input to program SURVIV (White 1983), parameterized with the model of interest (a model at least as general as that used to generate the data). For relatively large R_t , the conditional maximum likelihood estimates and standard errors produced represent the approximate expected values of the estimators and their standard errors. Models without estimability problems were conservatively identified when all estimators were unbiased to the fifth decimal place and had coefficients of variation $< 100\%$. For each case, we considered six or seven time periods, and computed expected cell frequencies based on $R_t = 500$ animals per time period. We generated data based on some combination of the following sets of parameter values: $\psi_i^{OO} \equiv 0.60$, $\psi_i^{UO} \equiv 0.70$, $\psi_i^{UO'} \equiv 0.81$; $\psi_i^{OO} \equiv 0$, $\psi_i^{UO} \equiv 0.70$, $\psi_i^{UO'} \equiv 0.81$; $\psi_i^{OO} = \psi_i^{UO} \equiv 0$, $\psi_i^{UO'} \equiv 0.70$; $\psi_i^{OO} \equiv 0.70$, $\psi_i^{UO} = \psi_i^{UO'} \equiv 0.55$; $\psi_i^{OO} \equiv 0$, $\psi_i^{UO} = \psi_i^{UO'} \equiv 0.70$; $S_i^O \equiv 0.75$, $S_i^U \equiv 0.85$; $S_i^O = S_i^U \equiv 0.80$; $p_i^* \equiv 0.64$. We do not lose any generality in assessing models with time-specific parameters by choosing values that are equal over time. For the purposes of this exercise, to consider p_i^* known is equivalent to assuming that this parameter is estimated from a source of data other than one observation period per time period (e.g., the robust design). The SURVIV code used in these exercises, as well as documentation on running it, can be found online.²

Results

Results of this analytic-numeric exercise are summarized for both second-order (Table 1) and first-order (Table 2) Markovian transition probabilities. In addition to the general case of stochastic movement, we include cases of partial determinism, motivated by examples in which breeders become obligate nonbreeders for one or two years. In the tables, a “Y” indicates that all parameters were estimable, with the possible exception of some confounding in the last period of the study, a phenomenon common to most open-population CMR models with time-specific parameters (e.g., see Lebreton et al. 1992).

² URL: www.mbr-pwrc.usgs.gov/software/unobservable.html

TABLE 1. Estimability of parameters using capture–recapture models with second-order Markovian emigration and state-dependent survival, when there is one observable and one unobservable state.

Model	Models by parameter type			Estimability by case†		
	Transition	Survival	Detection	General	1-yr obligate nonbreeder‡	2-yr obligate nonbreeder§
1	$\psi_i^{OO}, \psi_i^{UO}, \psi_i^{UO'}$	S_i^O, S_i^U	p_i^*			
2			p_i^*			
3			known			Y¶
4		S_i^O, S_i^U	p_i^*			
5			p_i^*			
6			known			Y
7		$S_i^O = S_i^U$	p_i^*			Y
8			p_i^*			Y
9			known	Y	Y	Y
10	$\psi_i^{OO}, \psi_i^{UO}, \psi_i^{UO'}$	$S_i^O = S_i^U$	p_i^*			Y
11			p_i^*	††	Y	Y
12			known	Y	Y	Y
13		S_i^O, S_i^U	p_i^*			
14			p_i^*			
15			known			Y
16		S_i^O, S_i^U	p_i^*			
17			p_i^*			
18			known			Y
19	$\psi_i^{OO}, \psi_i^{UO}, \psi_i^{UO'}$	$S_i^O = S_i^U$	p_i^*			Y
20			p_i^*	††		Y
21			known	Y	Y	Y
22		$S_i^O = S_i^U$	p_i^*	††	Y	Y
23			p_i^*	††	Y	Y
24			known	Y	Y	Y

† Y indicates that all parameters are estimable with the usual possible exception of confounding of some parameters in the last period of a study.

‡ Implies $\psi_i^{OO} \equiv 0$.

§ Implies $\psi_i^{OO} = \psi_i^{UO} \equiv 0$.

|| Implies that detection probability can be estimated from another source of information, such as multiple secondary sampling periods within each primary time period (i.e., Pollock's [1982] robust design).

¶ Generally does not work, with the exception of some special cases, for example, (S_i^O, S_i^U) and (S_i^O, S_i^U) .

†† Unbiased, but $cv > 100\%$ for at least some parameters.

No partial determinism in transitions.—Parameters are only fully estimable in this case when detection probability is known from other sources of information. If such extra information is available, as when data are collected under the robust design, and if survival rate is the same for those in the observable and unobservable states, then these survival rates and second-order Markovian transition probabilities can be estimated. The most general model where this works is $(\psi_i^{OO}, \psi_i^{UO}, \psi_i^{UO'}, S_i^O = S_i^U, p_i^* \text{ known})$, which is model 9 in Table 1. This model is a generalization of the Markovian model of Kendall et al. (1997) and Kendall and Bjorkland (2001), represented as model 33 in Table 2, which only allowed for first-order Markovian transitions, and the model of Schwarz and Stobo (1997), which assumed that observability is a completely random process (i.e., $\psi_i^{OO} = \psi_i^{UO} = \psi_i^{UO'}$).

A caveat with this general case of second-order Markovian transition is that even with the relatively large sample sizes and survival and detection probabilities we used, the expected proportional standard error on the transition probability estimates was large, exceed-

ing 40% for $\hat{\psi}_i^{UO}$. Therefore it is not clear how useful this particular model will be for estimating transition probabilities, and this topic merits further investigation. Constraining this model to first-order Markovian transitions, or introducing partial determinism in transition probabilities, as we will discuss, improves this precision.

Breeders become obligate nonbreeders for one year.—The scenario in which only breeders are observable provides a good example of the problem of an unobservable state. In some cases, breeders in one year will always skip breeding in the next year. Hawks-bill sea turtles provide an example in which no female that nests in a given year is found nesting in the following year (Richardson et al. 1999). In some cases, only successful breeders forego breeding in the following year, such as with some albatross (*Diomedea* and *Phoebastria* spp.; Weimerskirch et al. 1987). Rothery and Prince (1990) demonstrate potential bias in survival estimates in the face of this phenomenon when the Cormack-Jolly-Seber (CJS) method (see Seber 1982) is used.

TABLE 2. Estimability of parameters using capture–recapture models with first-order Markovian transitions and state-dependent survival, when there is one observable and one unobservable state.

Model	Models by parameter type			Estimability by case†	
	Transition	Survival	Detection	General	1-yr obligate nonbreeder‡
25	$\psi_i^{OO}, \psi_i^{OU} = \psi_i^{UO'}$	S_i^O, S_i^U	p_i^*		
26			p_i^*		
27			known§		
28			p_i^*		
29			p_i^*		
30			known		
31		$S_i^O = S_i^U$	p_i^*		
32			p_i^*	††	Y
33		$S_i^O = S_i^U$	known	Y	Y¶
34			p_i^*		Y
35			p_i^*	††	Y
36			known	Y	Y
37	$\psi_i^{OO}, \psi_i^{OU} = \psi_i^{UO'}$	S_i^O, S_i^U	p_i^*		
38			p_i^*		
39			known		
40		S_i^O, S_i^U	p_i^*		
41			p_i^*		
42		$S_i^O = S_i^U$	known		
43			p_i^*	††	Y
44			p_i^*	††	Y
45		$S_i^O = S_i^U$	known	Y	Y
46			p_i^*	††	Y
47			p_i^*	††	Y
48			known	Y	Y

† Y indicates that all parameters are estimable with the usual possible exception of confounding of some parameters in the last period of a study.

‡ Implies $\psi_i^{OO} \equiv 0$.

§ Implies that information on detection probability is available from another source, such as multiple secondary sampling periods within each primary time period.

|| Model described in Kendall et al. (1997).

¶ Model used in Kendall and Bjorkland (2001).

†† Unbiased, but $CV > 100\%$ for at least some parameters.

What can be done with respect to estimating demographic parameters in this special case? As indicated in Table 1, when transitions are second-order Markovian, the robust design or some other source of information on detection probabilities is generally required. Exceptions include models 11, 22, and 23, where survival probabilities and either detection or transition probabilities must be constant across time. In addition, survival rates must be identical for animals in the observable and unobservable states. The need for the robust design does not present logistical problems for nesting sea turtles. Many nesting beach studies consist of several sampling occasions within a breeding season, and due to re-nesting, there is ample opportunity to detect a given female in more than one sampling period per season.

To our knowledge, most albatross banding studies have not been conducted using the robust design, although it seems to us that multiple sightings of an individual per season would be feasible for a bird whose breeding cycle exceeds 200 d in many cases (Weimerskirch et al. 1987). Another possible sampling scenario that would permit estimation under this general model is based on the assumption that detection

probability of breeders during the breeding season is 1.0. We have found that this assumption has been made frequently and then disproven when the right kind of information became available. Kendall and Bjorkland (2001) found this assumption to be nearly true for a nesting population of hawksbill sea turtles, based on robust design data, but the availability of this type of data made the assumption unnecessary. Given how accessible albatross are to capture, this assumption might be tenable for smaller breeding populations (Weimerskirch et al. 1987). In that case, one could model breeding probability as a second-order Markov process.

For first-order Markovian transition probabilities where observable animals become obligate unobservable animals for one time period ($\psi_i^{OU} = 1$), the number of possibilities for estimation increases (Table 2). For some models where survival rate is the same for observable and unobservable animals, detection probability can be estimated directly and does not need to be known either from the robust design or by assumption. Specifically, one sampling occasion per time period is sufficient if either detection probability or survival rate is assumed constant across time (models [$\psi_i^{OO} = 0, \psi_i^{OU} = \psi_i^{UO'}, S_i^O = S_i^U, p_i^*$] and [$\psi_i^{OO} = 0,$

TABLE 3. Comparison of estimates and their precision for two approaches (robust design and pooling captures within a year) to estimating survival and breeding probabilities for a capture-recapture study of adult female hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua, 1987–1996.

Parameter	Estimate (1 SE)	
	Robust design	Pooled within year
S_t	0.95 (0.013)	0.94 (0.015)
ψ_{89}^{UO}	0.80 (0.100)	0.80 (0.161)
ψ_{90}^{UO}	0.40 (0.082)	0.40 (0.172)
ψ_{91}^{UO}	0.60 (0.075)	0.58 (0.140)
ψ_{92}^{UO}	0.68 (0.086)	0.66 (0.166)
ψ_{93}^{UO}	0.49 (0.083)	0.49 (0.193)
ψ_{94}^{UO}	0.46 (0.079)	0.45 (0.172)
ψ_{95}^{UO}	0.61 (0.089)	0.59 (0.212)
ψ_{96}^{UO}	0.34 (0.079)	0.34 (0.092)

$\psi_t^{UO} = \psi_t^{UO'}$, $S_t^O = S_t^U$, p_t^*], respectively, in Table 2). Fujiwara and Caswell (2002) noted this possibility and applied it to a specific case.

This is certainly a great advantage when these conditions are met. It removes the bias that is introduced in estimates for all parameters under a model based on one sample per time period (i.e., modified CJS type models) when transitions to/from an unobservable state are not completely random (Kendall et al. 1997). However we still recommend finding ways to employ the robust design, because it requires fewer assumptions (e.g., it allows full time dependence in parameters) and uses information more efficiently. In addition, at least five time periods are required in the absence of ancillary information on p_t^* , in order to use these models. For fewer time periods, the number of parameters exceeds the number of multinomial cells (i.e., sufficient statistics) and estimation is not possible.

To illustrate the advantage of using the robust design, we reanalyzed the hawksbill sea turtle data that were analyzed originally using the robust design in Kendall and Bjorkland (2001). Briefly, these data are from an ongoing nesting study on Long Island, a small island several kilometers offshore of Antigua, in the eastern Caribbean. Observers search the beach for signs of females that have come out of the surf to lay a clutch of eggs. They wait until the female is on the nest and then inspect her for a mark (tag or a notch on her shell) that uniquely identifies her. If there is no mark, they apply a tag to the front flipper and notch her shell. Observers are out every night from mid-June to mid-November (Richardson et al. 1999). Kendall and Bjorkland (2001) broke this sampling effort into half-month intervals and analyzed the data for 1987–1996 under model ($\psi_t^{OO} = 0$, $\psi_t^{UO} = \psi_t^{UO'}$, $S_t^O = S_t^U$, p_t^* known), the most parsimonious based on AIC_c (Burnham and Anderson 1998). We pooled these detailed capture histories into histories that simply recorded whether or not a given female was seen in year t . For direct comparison against the robust design analysis, we used model ($\psi_t^{OO} = 0$, $\psi_t^{UO} = \psi_t^{UO'}$, $S_t^O = S_t^U$, p_t^*).

The results of estimation under both approaches are shown in Table 3. Point estimates are almost identical under the two approaches, which is not surprising. The standard errors for survival estimates are also similar, but the standard errors for breeding probability estimates are approximately doubled when within-year capture information is ignored. The pattern of the results is consistent with that of Kendall et al. (1995), who showed that using the robust design in lieu of the Jolly-Seber method improved precision in estimates of detection probability (and hence abundance) considerably, but had little effect on the precision of survival rate estimates. Because transitions to and from the unobservable state are tied up statistically with detection probability (Kendall et al. 1997), a greater improvement in the precision of breeding probability estimates vs. survival probability estimates could be expected. However, Kendall and Bjorkland (2001) also estimated that $p_t^* \approx 1$, with capture probabilities for individual sampling occasions on the order of 0.90. Because one might expect a priori that the extra information provided by the robust design is not as great when detection probability is very high, the difference in precision indicated in Table 3 is especially noteworthy.

Breeders become obligate nonbreeders for two years.—There are some situations in which it is reasonable to assume that an observable animal will become obligate unobservable for two time periods thereafter. Fujiwara and Caswell (2002) discuss this case for right whale (*Eubaleaena* spp.) populations.

As in the other cases that we have considered, employing the robust design and assuming that survival rates are the same for the observable and unobservable states, all parameters are estimable (model 9 in Table 1). Fujiwara and Caswell (2002) made the interesting and useful discovery that transition/survival and detection probabilities can be estimated from one sample per year (i.e., no robust design or assumption of $p_t^* \equiv 1$), in their case assuming that all parameters are constant across time. We have found that time restrictions can be relaxed somewhat, requiring only that detection probability or survival probability be constant across time (models 8 or 10 in Table 1). Even more noteworthy, if the robust design is used, the extra determinism in this case allows one to estimate separate survival rates for those in the observable and unobservable states, assuming that either transition probabilities or survival rates are equal across time (models 6 and 15 in Table 1). We further investigated the case of model ($\psi_t^{OO} = \psi_t^{UO} = 0$, $\psi_t^{UO'} = S_t^O$, S_t^U , p_t^* known) and found that it did not work in general, but did for certain cases where $S_t^O \equiv S_t^O$ or $S_t^U \equiv S_t^U$. Where these special cases seem reasonable, estimability could be investigated further.

Completely random transitions.—We also evaluated the case in which observability is a completely random process, with no Markovian structure. Burnham (1993) showed that this general case results in total confound-

ing of observability and detection probability when there is only one sampling occasion per time period. Kendall et al. (1997) used the robust design to resolve the confounding when survival rate is the same for observable and unobservable animals (model $\psi_i^{OO} = \psi_i^{UO} = \psi_i^{UO'}$, $S_i^O = S_i^U$, p_i^* known). We found no model with state-specific survival rate that permitted estimation. When survival rates are not state specific, they can be estimated under the CJS method, but if transitions are of interest, then the robust design or $p_i^* \equiv 1$ is required.

DISCUSSION

We have provided a general framework within which to consider the phenomenon of temporary emigration, modeled as transitions between an observable and unobservable state. Motivated by cases in which species skip years of breeding, we started with a model that includes constrained second-order Markovian transitions, a state-dependent survival process, and time-dependent detection probabilities, but that contains too many confounded parameters to be useful for estimation. However, we arrived at models that are useful for estimation by either (1) imposing time constraints, (2) reducing the order of the state-dependent nature of transition or survival processes, (3) introducing partial determinism to the transition process, or (4) deriving estimates of detection probability from another source such as Pollock's robust design. Although a subset of these cases has been considered before by Kendall and Nichols (1995), Kendall et al. (1997), Schwarz and Stobo (1997), and Fujiwara and Caswell (2002), these cases had not been linked previously by a single conceptual framework. Within this framework, we have explored the interesting discovery by Fujiwara and Caswell (2002) that transitions to and from an unobservable state sometimes can be accounted for under a classic open-population CMR design (i.e., one sampling period per time period of interest). Specifically, we identified cases in which this approach can be exploited, and compared results with those based on the robust design.

We have discovered that there is more than one reasonable model where parameters can be estimated without the robust design, as long as there is some partial determinism in transition probabilities. However, as indicated in Tables 1 and 2, when the robust design is employed (or when one can reliably assume $p_i^* \equiv 1.0$), far less restrictive assumptions are required. Under the robust design, partial determinism in transition probabilities is not required for first-order or, to some extent, second-order Markovian transitions, and time constraints are either not required or are less restrictive than with one sample per time period.

In addition, estimates of survival probability were often well behaved (small bias with reasonable precision) when $S_i^U = S_i^O$, even for models where other parameters were not estimable. However, we do not rec-

ommend relying on this robustness without further research, using a range of parameter values and sample sizes. Simulation should be used in this case.

Perhaps the most interesting discovery is the case of the following models:

$$(\psi_i^{OO} = \psi_i^{UO} = 0, \psi_i^{UO'}, S_i^O, S_i^U, p_i^* \text{ known})$$

$$(\psi_i^{OO} = \psi_i^{UO} = 0, \psi_i^{UO'}, S_i^O, S_i^U, p_i^* \text{ known})$$

where survival rate depends on which state the animal occupies. The general assumption of equal survival rates for observable and unobservable animals is a potentially very restrictive one, a consequence of having an unobservable state (i.e., unobservable animals are not released and therefore their survival cannot be directly associated with that state). W. L. Kendall and C. S. Jennelle (*unpublished data*) found several scenarios in which estimation is robust to violation of this assumption, but nevertheless, the discovery of cases in which the assumption is unnecessary should prove useful.

The use of deterministic transitions to simplify modeling and permit estimation of quantities that would not otherwise be estimable is not unique to the issue of temporary emigration. For example, age is a dynamic state variable, but it is characterized by deterministic transitions in the usual case in which the interval between sampling periods corresponds to the time period required to make the transition to the next age class. Thus, an animal of age v in year i is known to be of age $v + 1$ in year $i + 1$. Because of this determinism, the probabilities corresponding to the m_{ij} statistics under the multiple-age models of Pollock (1981) and Loery et al. (1987) can all be written as products of parameters, with no sums of probabilities representing multiple paths (multiple possible states when the individual was not observed). Thus, multiple-age models are much simpler in many ways than fully stochastic multi-state models. We have not incorporated age into the models that we have considered here, but anticipate that our conclusions would also apply to age-dependent versions.

We have discussed exploiting extra information on detection probability through the robust design. Other types of ancillary data can be used to supplement CMR data and reduce or eliminate confounding. For example, Powell et al. (2000) used location information from radio telemetry data to directly estimate movement of Wood Thrushes (*Hylocichla mustelina*) to an area outside that covered by their CMR study, thus permitting the CMR data to contribute information useful in estimating survival. Burnham (1993; also see Szymczak and Rexstad 1991) used band recoveries and CMR data in a single joint analysis. Under the assumptions that waterfowl are never unobservable with respect to the recovery process (i.e., bands from dead birds always have a chance of recovery), and that emigration from a banding location is permanent, Burnham (1993) es-

timated survival and emigration simultaneously. Barker (1997) extended Burnham's work to assume that incidental observations are possible for any animal regardless of its location, and Barker (1995) removed the assumption that emigration is permanent (with constraints over time). Lindberg et al. (2001) combined Burnham's model with the robust design to estimate temporary movement to one type of unobservable state (nonbreeder still associated with breeding area) and permanent movement to another unobservable state (failed fidelity to a breeding area) for Canvasback Ducks (*Aythya valisineria*).

Our assessment here has been primarily theoretical in the sense that we were interested in what parameters could be estimated under various model structures and types of available data. Even for the models where we found no problems with estimability, small sample size and sparseness (e.g., empty cells) could still cause estimability or precision problems. Methods such as those of Catchpole and Morgan (1997) could be used to assess estimability in the face of both model structure and sparseness problems.

As with any ecological study, the investigator should use prior notions of parameter values to simulate the expected demographic and capture process, to determine the design and sampling effort necessary to minimize bias and achieve desired precision. Using program SURVIV (White 1983), estimability problems, due either to model structure or data sparseness, usually manifest themselves through singularity of the variance-covariance matrix, or at least very large variances (i.e., proportional standard errors of well over 100%). When, $\psi_i^{OU} > \psi_i^{UO}$, precision of ψ_i^{UO} tends to be especially poor because animals are not available for detection very often.

Despite the fact that, with some assumptions, transitions to and from an unobservable state are a tractable estimation problem, it is still preferable to sample all potential locations of marked animals. This would permit the use of multi-state models (e.g., Hestbeck et al. 1991, Spendelov et al. 1995), which allow for state-specific survival rates and both first- and second-order Markovian transitions (Brownie et al. 1993). When there are multiple observable states and at least one unobservable state, the estimation problem becomes even more complicated, but not necessarily intractable.

Where transitions to an unobservable state are inevitable, we recommend exploiting partial determinism where possible, but in general strongly recommend the use of Pollock's (1982) robust design in setting up a study, employing multiple well-defined secondary sampling periods for each primary time period of interest. The advantages of this design are numerous and include some beyond the scope of this paper (e.g., Pollock 1982, Pollock et al. 1990, Kendall and Pollock 1992, Kendall et al. 1995).

Software exists for computing estimates under most of the tractable models discussed here. Programs

(available online) that can be useful include RDSURVIV, ORDSURV, TURTURNS, and MSSURVIV,³ and MARK.⁴ MSSURVIV and its counterpart in MARK can be useful for the case of partially deterministic transitions without robust design data.

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³ URL: <www.mbr-pwrc.usgs.gov/software>

⁴ URL: <www.cnr.colostate.edu/~gwhite/software.html>

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